

Evolving Evolutionary Psychology

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Which evolutionary theory can best benefit psychological theory, research, and application? The most well-known school of evolutionary psychology has a narrow conceptual perspective (a.k.a., “Narrow Evolutionary Psychology” or NEP). Proponents of NEP have long argued that their brand of evolutionary psychology represents a full-fledged scientific revolution, with Buss (2020) recently likening NEP’s scientific impact to that of a Copernican or Darwinian paradigm shift. However, NEP stands on two traditions that are now the subjects of serious debate and revision: the neo-Darwinian adaptationist framework within evolutionary biology, and the computationalist “mind-as-computer” framework within cognitive science. Although NEP calls itself revolutionary, the significant revolutions taking place today in both evolutionary biology and cognitive science reveal NEP to be rooted in the orthodoxies of the past. We propose a more inclusive, developmental evolutionary psychology theory (DEPTH) better suited for our field in multiple ways, from acknowledging epigenesis to incorporating developmental science. To discern appropriate baselines for human nature and for human becoming, one must integrate developmental neuroscience, anthropology, and cognitive archeology. To be of value in addressing and remedying the challenges facing humanity, psychological theories must recognize the central importance of our plasticity, evolved developmental niche, and deep history.


Public Significance Statement


Understanding humans and our behavior requires unpacking our evolutionary heritages and developmental pathways. We inherit much more than genes. Biology, environment, and culture are seamlessly intertwined, in both individual development and evolution. Every individual constructs their personhood through real-time engagement with the world, so it matters what kind of relational experiences the individual has. In contrast to the most prominent evolutionary psychology theory that emphasizes the stranglehold of humanity’s evolutionary past, a developmental evolutionary psychology theory orients to dynamic development in the present, taking epigenetics and plasticity seriously. This approach is better able to guide research and practice, and free people from the disempowering belief in biological determinism.


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Few psychologists would seriously question the central role of an evolutionary framework in explaining psychological functioning. In fact, evolutionary theory has long informed efforts in psychology to understand mind and behavior, from the recapitulationist-inspired doctrines of G. Stanley Hall and Sigmund Freud to the ethological frameworks of Konrad Lorenz and John Bowlby (Boring, 1950). Proponents of modern evolutionary psychology celebrate the field’s empirical yield, its theoretically driven hypothesis generation, the novelty of its predictions, and the heuristic value of its interpretative framework; these contributions are lauded as clear demonstrations of



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evolutionary psychology's invaluable role within psychological science (e.g., Buss, 1999; Confer et al., 2010; Lewis et al., 2017; Tooby & Cosmides, 2015). Many proponents even proclaim that evolutionary psychology is uniquely positioned to conceptually unify psychology (Buss, 2020; Confer et al., 2010).

Maintaining an evolutionarily informed psychology is critically important, but is the current field of evolutionary psychology up to the task? The broad discipline of evolutionary psychology is a blend of several diverse applications of evolutionary theory to human mind and behavior, including Human Behavioral Ecology, Cultural Evolution (including gene-culture coevolution theory), Social Constructivist approaches, Evolutionary Developmental Psychology, and Developmental Systems approaches (e.g., Bjorklund & Pellegrini, 2002; Gottlieb, 1992; Griffiths & Gray, 1994; Gurven, 2018; Moore, 2006; Scher & Rauscher, 2003; Sear et al., 2007). Ploeger et al. (2008a) aptly described evolutionary psychology, in this most general sense, as “more a collection of point of views [sic], which are not necessarily consistent with one another, than it is a coherent theory” (p. 41). Indeed, this collection of viewpoints reveals some deep-seated conceptual differences in perspective over ideas as foundational as the role that natural selection plays in evolution (Heyes, 2000; Scher & Rauscher, 2003). Too much conceptual heterogeneity and even metatheoretical division are evident in this broadly construed evolutionary psychology to adequately unify psychological science.

In contrast, one branch of evolutionary psychology has proffered a conceptually unified platform that its adherents tout as “revolutionary”—a grand metatheory not just for all of evolutionary psychology but for all of psychological science

(Buss, 2015, 2020; Tooby & Cosmides, 2015). This more narrowly defined evolutionary psychology entertains its fair share of theoretical debates (e.g., debates over the extent of modularity and over domain-specificity in human psychological mechanisms), but these debates unfold within a shared conceptual framework of ideas concerning the nature of the evolutionary process and psychological functioning (Confer et al., 2010). Nonetheless, this shared conceptual framework has also inspired decades-long “vigorous opposition” (Buss, 2020, p. 5) from critics both within and outside of psychological science, including from those who consider themselves members of the broad evolutionary psychology community (e.g., Barrett et al., 2014; Scher & Rauscher, 2003; Stotz, 2014).

As the most prominent public face of the field, this narrower brand of evolutionary psychology—dubbed “narrow evolutionary psychology” (NEP) by Scher and Rauscher (2003)—continues to represent what most psychologists consider to be “mainstream” evolutionary psychology (Confer et al., 2010; Lewis et al., 2017; Ploeger et al., 2008b). Proponents of NEP tout the conceptual pedigree of their approach by tracing its origins to particular 20th century developments in the disciplines of evolutionary biology and cognitive science (Tooby & Cosmides, 2015). From evolutionary biology, NEP has embraced adaptationism and inclusive fitness theory, privileging natural selection as a major cause of current human functioning, and privileging genes as principal units of selection. From cognitive science, NEP has embraced computationalism and its information-processing conceptualization of the mind/brain. As foundational principles, adaptationism and computationalism establish the shared conceptual framework within which NEP operates, a framework that NEP proponents espouse as a “cogent metatheory for understanding the complexities of the human mind” (Buss, 2020, p. 1).

A close look at NEP's foundational principles, however, shows them to be inconsistent with contemporary thinking in both evolutionary biology (e.g., Bolhuis et al., 2011) and cognitive science (e.g., Newen et al., 2018). NEP's core assumptions concerning the nature of the evolutionary process rely on adaptationist ideas, while its core assumptions concerning the architecture of the human mind rely on computationalist ideas. However, adaptationism and computationalism—the conceptual “pillars” that support NEP—are now the subject of serious, mainstream debate and fundamental revision within the very scientific disciplines to which NEP owes its conceptual allegiance. This raises critical questions about the adequacy of NEP's conceptual framework and the extent to which it can do justice to the complexities of the human mind.

A useful evolutionary psychology needs to be grounded in conceptual advances, not just empirical output. At the level of sheer empirical generativity, few can seriously challenge NEP's prowess. But data, findings, and the theories that frame them are of inherently limited value when they emanate from flawed conceptual presuppositions. As Hogan



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(2001) has succinctly noted, “all the empiricism in the world cannot salvage a bad idea” (p. 27). As we argue below, within both evolutionary biology and cognitive science, the constructs of gene-centered adaptationism and computationalism are looking more and more like bad ideas.

Fortunately, as we have indicated, alternative approaches to evolutionary psychology exist, ones that can advance the field beyond NEP’s increasingly antiquated conceptual roots (e.g., Barrett et al., 2014; Buller, 2005; Lickliter & Honeycutt, 2013; Scher & Rauscher, 2003). But to adequately inform psychological science, evolutionary psychology needs a new, unifying set of “first principles” abstracted from some of the conceptual diversity endemic to evolutionary psychology, broadly construed. In what follows, we first examine NEP, the most prominent version of evolutionary psychology, and describe how its conceptual foundations are currently mired in controversy. Then we address alternative, up-to-date perspectives that should inform the shape of the bedrock foundations of any emerging evolutionary psychology. Finally, we discuss what kinds of alternative principles better meet the needs of the day theoretically and practically, identifying more appropriate baselines for human normality, with attention to critical developmental processes. We conclude with a discussion of how a developmental evolutionary psychology better addresses contemporary and urgent psychological questions.

Pillar I: Neo-Darwinism, Adaptationism, and Contemporary Evolutionary Biology

Neo-Darwinism, or the “Modern Synthesis” (Huxley, 1942), was the theory that defined evolutionary biology

through much of the 20th century (e.g., Laland et al., 2015; Pigliucci, 2007). This understanding of evolution blended ideas drawn from Darwinian views of evolution and Mendelian views of genetics. It represented a population-level approach to evolutionary change, emphasizing the principles of natural selection and adaptation, differences in survival and reproduction (fitness), and heredity. Collectively, these features of the neo-Darwinian approach supported a narrative in which environments “pose” well-defined problems for organisms to solve, and the individuals best able to survive and reproduce in those environments are the individuals whose traits represent the best “adaptation” to the problems posed. Changes from one generation to the next in a population’s genetics occur as “genes for adaptive traits” spread by natural selection through succeeding generations. Unabashedly gene-centric (see Mayr, 1961, 1982), the Modern Synthesis promoted a strong form of selectionism—the belief that natural selection, acting on gene frequencies in a population, is the primary cause of both evolutionary change and the stability of species-typical traits observed within populations.

Neo-Darwinism remains the primary theoretical foundation underlying contemporary biology (Mayr, 2001); it has proven to be a remarkably flexible theory able to generate and explain an enormous amount of empirical data (Coyne, 2009; Ellegren & Sheldon, 2008). However, scientists and philosophers concerned with *theoretical* biology have been expressing concerns about neo-Darwinism since at least the late 1950s (Gould, 1980, 2002; Jablonka & Lamb, 1995; Moore, 2002; Noble, 2015; Pigliucci, 2007; Tanghe et al., 2018; Waddington, 1957). These concerns have often focused on a consequence of the fact that the 20th century architects of the Modern Synthesis—knowing that they were not yet able to explain how developmental processes give rise to phenotypes—chose to finesse their predicament by defining evolution as a process that affects gene frequencies across populations (Moore, 2002). This move allowed them to construct neo-Darwinism as a theory strictly about the roles of genes in evolution (Jablonka & Lamb, 1995). As a result, neo-Darwinism ignores the role of development in evolution, despite the acknowledged fact that developmental processes should play a central role in any comprehensive theory of biology (Moore, 2008a). To many theorists, this situation seems untenable, suggesting that traditional neo-Darwinism will not be able to stand the test of time (e.g., Blumberg, 2009; Laland et al., 2015; Noble, 2015; Stotz, 2014; Tanghe et al., 2018). Indeed, *Nature* recently published a debate titled “Does Evolutionary Theory Need a Rethink,” which raised serious concerns about the neo-Darwinian perspective (Laland et al., 2014; Wray et al., 2014). Nonetheless, NEP’s evolutionary concepts remain rooted in the latter, contested theoretical framework. Consistent with the neo-Darwinian tradition, proponents of NEP continue to privilege genes as the primary targets of natural selection.



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NEP and the Conceptual Agenda of Neo-Darwinism

According to neo-Darwinism, natural selection is what “delivers” adaptations across generations by means of gene selection; this is the central idea underlying adaptationist thinking. In other words, natural selection is characterized as a mechanical, antecedent force, capable of shaping individual development by inherited mechanisms. Applying this to psychology, NEP theorists assume that psychological adaptations can be explained solely with reference to natural selection of genetic variations inherited from prior generations (Confer et al., 2010). For example, innate rules of perception and cognition are presumed to be prespecified in the genes as a result of selection pressures in our ancestral past (Tooby & Cosmides, 2015). This prespecification assumption central to NEP allows its proponents to claim that each human comes into the world with “innate ideas or a priori concepts” (Tooby & Cosmides, 2015, p. 7). However, this assumption that prespecifications for “evolved” human traits can exist in the genome—in advance of the real-time developmental processes that elicit said traits—is inconsistent with biologists’ current understanding that all physical and psychological traits must be constructed during individual development, whether those traits have an acknowledged evolutionary history or not (Gottlieb, 1992; Lickliter, 2008; Lickliter & Berry, 1990; Oyama, 1985). Specifically, all phenotypes come into being via developmental processes that involve the coaction of deeply entangled biological and nonbiological factors (e.g., DNA, epigenetic marks, nutritional factors, and social environments, to name just a few) that mutually influence one

another as development takes place. Simply put, human capacities are neither genetically nor environmentally specified, but emerge within processes of development (Ingold, 2006). Contemporary evolutionary biology is well aligned with this fact, particularly evolutionary developmental biology (see Hall, 2012). NEP, however, is not.

In contrast to their sociobiological predecessors (Wilson, 1975), NEP proponents claim to not be gene-centric and, therefore, to not promote genetic determinism. Rather, they endorse a form of weak interactionism in which phenotypic development is thought to reflect the additive operation of two separate sources of information, one that is internal, formative, and relatively fixed (genes) and one that is external, supportive, and relatively variable (environment). This conceptual separation of causal factors that arise from genes and those that arise from the environment is, however, indefensible in light of contemporary biological theories and data (Moore, 2002). It is now widely understood across the life sciences that gene activity is regulated by systemic factors in and above the levels of molecular and cellular activity, and that many of these factors originate outside of the organism. As a result, genetic and environmental factors cannot be meaningfully partitioned (Lickliter, 2009; Moore, 2015).

Most biologists are no longer preoccupied with, and are even skeptical of, adaptationist thinking, and the closely associated idea that genes hold privileged status in the developmental construction of traits. Any sharp focus on adaptationism has been criticized by biologists and philosophers of science since the late 1970s (e.g., Buller, 2005; Gould & Lewontin, 1979; Richardson, 2007; Shapiro & Epstein, 1998) and much more nuanced understandings have since permeated biological theory (Godfrey-Smith, 2001; Millstein, 2007; Orzack & Forber, 2017). Biologists now hold that many phenotypes are better explained with reference to nonadaptive forces. In this “pluralism” perspective, adaptation is considered only one cause of a trait’s evolution; other factors include developmental constraints and historical contingency, which are nonadaptive forces. In other words, natural selection, central to adaptation, is now recognized by biologists as only one of several mechanisms of evolutionary change. Nevertheless, for proponents of NEP, “identifying the [evolved] adaptive functions of psychological mechanisms” has continued to be an “indispensable” goal since the 1980s (Buss, 2020, p. 2). Consequently, NEP and its underlying conceptual tenets have been the subject of a great deal of criticism (e.g., Bolhuis & Wynne, 2009; Lloyd & Feldman, 2002; Rose & Rose, 2000), with a range of arguments challenging this approach. (Trenchant critiques leveled at NEP are available in Buller, 2005; Fodor, 2000; Gould, 2002; Lewontin, 2000; Lynch, 2007; and Richardson, 2007.) We now consider how, even beyond the limitations of adaptationism, the neo-Darwinian framework within evolutionary biology on which the



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pioneers of NEP built their field is now being disputed among evolutionary biologists themselves.

The Evolution of Evolutionary Biology and Its Challenge to Neo-Darwinism

The conceptual foundations of neo-Darwinism have been a source of debate within evolutionary biology since well before the emergence of NEP in the 1980s. In particular, contemporary biologists and philosophers of science are now focused on several phenomena and ideas that have collectively undermined the older—and in some cases, discredited—assumptions that are foundational for NEP theorists. Three important examples of these phenomena and ideas are: the blurred distinction between proximate and ultimate causes of phenotypes (Laland et al., 2013); the role of niche construction in evolution (Bolhuis et al., 2011; Laland et al., 2015; Lloyd & Feldman, 2002); and the importance of developmental plasticity to evolutionary change (e.g., Laland et al., 2014).

Proximate and Ultimate Causes of Phenotypes

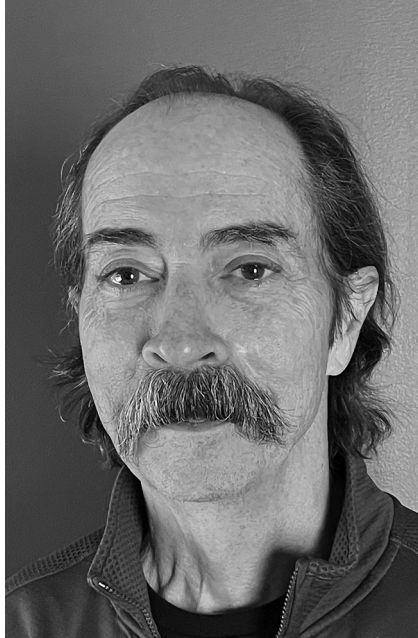
A conceptual cornerstone of NEP has been the dichotomization of causal explanation for phenotypic traits into phylogenetic (evolutionary) or ontogenetic (developmental) factors, operating on ultimate and proximate levels, respectively. Phylogenetic factors are assumed to have operated on the individual's ancestors and to have delivered to the current generation gene specifications for traits that are merely “read out” during development. In contrast, ontogenetic factors are understood to operate during the individual's development and to trigger

or interfere with the expression of the phylogenetically delivered gene-based specifications. Proponents of NEP claim they are concerned only with the ultimate causation of human behavior and its function or adaptive value (Buss, 1999; Gaulin & McBruney, 2004), allowing the field to effectively sidestep the role of development in understanding the phenotype.

However, converging evidence from the last 30 years of biological science, particularly from epigenetics and evolutionary developmental biology, indicates that the decoupling of proximate and ultimate levels of explanation is not tenable, because genetic and environmental contributions to development cannot be viewed independently (Lickliter & Berry, 1990). Instead, “proximate causes are themselves often also evolutionary causes” (Laland et al., 2015, p. 6), since “development is a direct cause of why and how adaptation and speciation occur” (Laland et al., 2014, p. 164); this is the case because developmental processes affected by niche construction and developmental constraints have been implicated in changes to both the rate and direction of evolution. NEP's continued application of the proximate/ultimate distinction, and its neglect of development, reify the misleading assumption that natural selection, acting on previous generations, delivers a set of genetic specifications (ultimate causes) to the current generation, and that contexts and experiences (proximate causes) independently trigger the unfolding of prespecified traits. In fact, genetic and experiential contributors to phenotypes are interrelated at all stages of development, and neglecting either type of factor leads to a profound distortion of how traits are built (Lickliter & Witherington, 2017; Moore, 2015). The architects of the Modern Synthesis—like the NEP theorists that followed them—assigned no role for developmental processes in evolution, but the discovery that developmental processes always affect the emergence of adaptive traits means that a new conceptualization of evolutionary explanation is needed.

Niche Construction

The neo-Darwinian idea that environments “pose” problems for organisms to solve has been undermined dramatically by the recognition that organisms are not exposed to environments at random and need not respond to their environments in a passive way. Instead, organisms effectively inherit many aspects of their environments from their parents (Griffiths & Gray, 1994; Lickliter, 2008; West & King, 1987). This is how manatees and minnows come to inhabit an aquatic environment while elephants and human beings come to inhabit a terrestrial environment. In addition, organisms play important roles in creating their environments. Some animals actively alter their habitats; for example, birds build nests, beavers build dams, humans build houses, and ants create gardens in which they grow their fungal food. All organisms also effectively “construct” their own environments in a more passive way, as Lewontin



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and Levin (1997) noted: “every terrestrial organism is surrounded by a shell of warm moist air produced by its own metabolism, a shell that constitutes its most immediate ‘environment’” (p. 97). Niche-construction theory has helped biologists acknowledge that evolution is not primarily about solving preexisting problems that have been “posed” to organisms. The challenges faced by individual organisms are often not independent of those same organisms, and even are commonly self-imposed. Accordingly, biologists now recognize that organisms have some influence over their own evolution, rendering questionable the idea that phenotypes reflect “solutions” to problems posed by environments that preexist and are independent of the organisms themselves. For humans, genes have coevolved with niche construction and culture. For example, the introduction of livestock and pastoralism enabled lactose toleration past childhood (Beja-Pereira et al., 2003) and shifted societies from matrilineal to patrilineal inheritance (Holden & Mace, 2003). Findings like this have led some theorists to surmise that cultural factors may play “an active, leading role in the evolution of genes” (Richerson et al., 2010, p. 8985). Because neo-Darwinists explicitly reject the idea that organisms can influence their own evolution, the phenomenon of niche construction again suggests that a different conceptualization of evolutionary explanation is needed.

Developmental Plasticity

In part because human brains are far more malleable than previously realized, NEP’s commitment to the idea of a genetically inherited universal human nature has not fared much better than the idea that we inhabit organism-independent,

problem-posing environments. Of course, most human brains share a remarkable number of similarities because 99.9% of the human genome is common to all of us (National Human Genome Research Institute, 2018) and all people develop in environments that share many similarities (e.g., all normal human developmental environments are characterized by the presence of caregivers, shelter, community support, the use of language, etc.). However, it is now clear that brains are remarkably plastic in the face of idiosyncratic experiences. For example, experience playing a musical instrument has significant effects on the structure and function of the brain (Pol-drack, 2018), and growing up with only a right cerebral hemisphere (i.e., with only half of a normal-sized brain) can nonetheless lead to relatively normal neurological, linguistic, and cognitive outcomes by adolescence (Asaridou et al., 2020). It is now apparent that our experiences affect our brains via the regulation of gene expression (Moore, 2017) and synaptic connectivity (Bolhuis et al., 2011), rendering the idea of a universal genetically inherited human nature increasingly unlikely. As noted below, humanity’s particular immaturity and plasticity in early life means that early experiences actually contribute to shaping the brain and its functions for the long term (e.g., Schore, 2019; Shonkoff & Phillips, 2000).

Importantly, developmental plasticity (along with developmental constraints) is now recognized as an essential contributor to evolutionary processes (Burman, 2019; Carroll, 2005; West-Eberhard, 2003). The discovery that cultural practices played a crucial role in the evolution of human DNA that contributes to adults’ ability to digest milk (Durham, 1991; Tishkoff et al., 2007; see also Moore, 2008b) strongly suggests that developmental plasticity permits the retention of juvenile phenotypes into adulthood when those phenotypes prove to be adaptive later in life. This sort of finding has led some theorists to argue that developmental plasticity might even “play a central directing role in evolution” (Wilson & Laland, 2016), an observation that has significant implications for evolutionary science, implications that encourage a rethinking of how we conceptualize evolutionary explanation.

The Extended Evolutionary Synthesis

Many of the aforementioned challenges to the tenets of neo-Darwinism are formally represented in the “Extended Evolutionary Synthesis” that has emerged in the last 15 years (Laland et al., 2015; Pigliucci, 2007). A few examples here will suffice. First, the Extended Evolutionary Synthesis (EES) challenges the traditional idea, still prevalent in the NEP literature, that natural selection is of paramount importance in explaining adaptation, and that selection pressures in the Pleistocene epoch are responsible for traits that characterize contemporary humans, even though today’s people emerged in the context of swiftly changing environments. In the clever words Bolhuis (2005) used to reject this outmoded idea, “we’re not Fred or Wilma” (p. 706). Second,

in contrast to the evolutionary model underlying NEP, proponents of the EES see organisms as actively involved in constructing their own environments, giving them some influence over their own evolution (Bolhuis et al., 2011; Laland et al., 2014, 2015). Third, the EES elevates the role of development in evolution, recognizing that developmental processes are responsible for the novel phenotypes on which natural selection can operate (Laland et al., 2014). Most of the many theorists who have called for revisions to the Modern Synthesis (e.g., Jablonka & Lamb, 2005; Moore, 2002, 2008b; Noble, 2006, 2015; Odling-Smee et al., 2003; Oyama et al., 2001; Pigliucci, 2007; Stotz, 2014; Witherington & Lickliter, 2016) agree that the adaptationism and the gene/environment dichotomy at the heart of NEP's evolutionary thinking is problematic, in that it distorts how evolutionary processes actually contribute to observed behavioral characteristics. Nevertheless, NEP theorists have mostly ignored niche construction and the role of development in evolution, and they have given short shrift to developmental plasticity. Most biologists would agree that the narrow focus on natural selection and adaptation that characterizes NEP is simply not reflective of contemporary evolutionary biology.

Pillar II: Computationalism and Contemporary Cognitive Science

The first pillar of NEP's approach—its neo-Darwinian, adaptationist focus—has been on questionable conceptual ground for some time, given widespread challenges that have arisen from within evolutionary biology itself. The second pillar of NEP's approach—computationalism, or the view of cognition as computation—has enjoyed much steadier support over the years, having informed and directed orthodox thought in cognitive science since the field's origins in the “cognitive revolution” of the 1950s (Bruner, 1990; van Gelder, 1995). NEP's signature appeal to inherited cognitive mechanisms that respond to ancestral rather than present environmental conditions is firmly rooted in this type of computationalism. Nonetheless, the computationalist pillar of NEP's approach is now showing signs of significant conceptual instability in the wake of a decade's worth of increasingly mainstream challenges from cognitive scientists themselves.

Computationalism's basic refrain has long assumed axiomatic status within many if not most psychological circles: all acts of cognition, even in their most rudimentary form, involve information processing functionally akin to what digital computers do. According to computationalist doctrine, cognitive activity intercedes between an organism's sensory inputs and behavioral, motoric outputs. Furthermore, cognitive activity is understood to consist of brain-based, subpersonal (e.g., outside of conscious awareness) mechanisms that operate, in rule-governed, algorithmic

fashion, on some form of representational content (e.g., internally stored information that “stands for” the world itself) to yield mandates for an organism's behavior. In effect, cognition is viewed as internalized problem-solving, a centralized, in-the-head, decision-making activity for controlling human behavior.

Computationalist models conceptualize cognitive functioning as “wholly realized by systems and mechanisms inside the brain,” as an intracranial activity isolated and detached from the continuous, real-time, fully interdependent perceptual-motor engagement of organisms with their environments (Kiverstein, 2018, p. 19; van Gelder, 1995; Wheeler, 2005). Brains, in other words, are viewed as housing cognitive functioning, but since brains have no direct access to the world that an organism inhabits, cognition is conceptualized as brains' computations on representational stand-ins for that world (Wheeler, 2005). Thus, for computationalists, an organism's behaviors do not constitute cognition; they simply reflect the products of an interiorized competence, of brain-based transformations of given sensory input values. This means that the intelligent behavior of an organism is necessarily preceded by, and distinct from, mechanisms of cognition themselves (Hutto & Myin, 2013). In computationalism, cognition acts on representational content, not on the world itself.

NEP and the Conceptual Agenda of Computationalism

Proponents of NEP wholeheartedly embrace the computationalism of orthodox cognitive science, so much so as to contend that “the brain is not just like a computer. It is a computer” (Tooby & Cosmides, 2015, p. 19). Notwithstanding the contrary view of neuroscientists (e.g., Panksepp & Panksepp, 2000), they argue that human brains consist of numerous, functionally specialized mechanisms, or information processing modules termed “evolved psychological mechanisms,” each of which evolved via natural selection to maximize inclusive fitness by solving recurrent problems characteristic of the environments early humans inhabited during the Miocene and Pleistocene geological epochs (Bjorklund & Pellegrini, 2002; Tooby & Cosmides, 2015). Such mechanisms, recently described by Buss (2020) as “procedures inside the head” that process environmental input and generate behavioral output (p. 3), thoroughly exemplify the interiorized problem-solving status of the computational mind.

It is important to note that NEP extends the bedrock principles of computationalism in two key ways. First, proponents take the detached, brain-based cognizer of orthodox cognitive science and further remove that “central executive” from interdependent organism–environment transactions that occur in real time. Proponents of NEP insist that human behavior is, in fact, frequently not a response to the present environment but to conditions that existed in our

prehistoric past, creating a somewhat irrational disconnect between present conditions and behavior. They suggest that information is processed using programs that act not on content corresponding to the current environment but on content related to ancestral conditions. By virtue of their contention that we are born with representational content corresponding to these ancestral conditions, proponents of NEP explicitly resurrect “the necessity of ‘innate ideas’” (Tooby & Cosmides, 2015, p. 56).

Second, by adopting the “massive” modularity hypothesis that is a core aspect of their theories, NEP proponents take the notion of modularity in cognitive functioning and magnify it considerably, positioning these “domain-specific, content-rich programs specialized for solving ancestral problems” as starting points for guiding and constraining information processing in human development (Tooby & Cosmides, 2015, p. 47). In this way, they carve out a distinctly nativist stance for the inherent modularity of computationalism (van Gelder, 1995). Modules are viewed as species-typical mechanisms that arise from genetic information (under “normal” environmental circumstances) and that serve as necessary preconditions for the experience of individual development. Each evolved module is treated as a preformed entity that appears independently of development, already laden with specific representational “knowledge” corresponding to those domains that presented distinct adaptive challenges for our ancestors (Tooby & Cosmides, 2015).

Computationalism’s traditionally dominant and largely unquestioned status in cognitive science has long provided NEP’s proponents with conceptual security—a security borne of the orthodox wisdom of the cognitive revolution. In recent years, however, computationalism itself—the very idea that cognition is computation—has become the subject of thoughtful challenges that are increasingly being given serious consideration within mainstream cognitive science.

The Rise of 4E Cognition—Embodied, Embedded, Extended and Enactive—and Its Challenge to Computationalism

Cognitive science in the 21st century has borne witness to a heightened period of self-critique (Newen et al., 2018). The assumption that cognition is information processing is not only open to active debate within cognitive science but is also at risk of being overthrown entirely.

Since the earliest days of computationalism’s ascendancy, repudiations of its various principles have arisen from the ranks of ecological psychology, dynamic systems theory, robotics, and phenomenologically inspired treatments such as enactivism (e.g., Brooks, 1991; Bruner, 1990; Gibson, 1979; van Gelder, 1995; Varela et al., 1991). Such longstanding repudiations, however, remained largely at the fringes of cognitive science. Not until the last decade or so have these

alternatives to computationalism become “a staple and familiar feature of the cognitive science landscape” (Hutto & Myin, 2018, p. 95), relegating computationalism to simply one alternative among many. Though evolutionary psychology, in either its broad or narrow formulations, need not embrace any of these alternatives in order to maintain internal consistency, it is simply no longer the case that its foundational cognitive theories must be aligned with computationalism.

Cognitive science today is taking seriously *4E cognition*, a family of perspectives that conceptually ground cognition in the embodiment of agents and their embeddedness in the world. The *Oxford Handbook of 4E Cognition* (Kiverstein, 2018; Newen et al., 2018) reveals three distinct, robust, and competing conceptualizations of mind: embedded, extended and enactive approaches. The “embedded” sector of today’s conceptual landscape remains committed to the view of cognition as brain-constituted and thoroughly computational in nature. Proponents of this territory, however, take seriously the complex mutuality of causal relations that obtain among brains (as seats of cognition), the bodies that house them, and the worlds in which those bodies are embedded (Kiverstein, 2018).

In contrast to embedded conceptualizations of mind, the “extended” sector of today’s 4E landscape rejects the “neurocentric internalism” of orthodox computationalism and, in the process, extends the boundaries of what counts as cognitive activity beyond the brain (Wheeler, 2014, p. 378). For proponents of this territory, facets of body and world (e.g., eye movements, hand gestures, tool use, writings, cultural artifacts) do not simply affect cognitive activity in a causal sense but can, in fact, be partially constitutive of cognitive activity itself (Newen et al., 2018). Extended theorists, however, still maintain a basic allegiance to the fundamentally computational nature of cognition; they merely distribute such computations (and their representational content) across brain, body, and world (Kiverstein, 2018; Wheeler, 2005, 2014).

Like their extended counterparts, the third, “enactive” sector of today’s 4E landscape rejects interiorized, brain-centric notions of mind. But enactive proponents go one step further by also rejecting the foundational status of computation and representation in the functioning of minds. Proponents of enactivism repudiate the purely intellectualized approach to cognition that computationalism entails (Hutto & Myin, 2013, 2017). In orthodox computationalism, activities of computation resemble logical and mathematical operations, modeled after the deliberative, calculation-based decision making that constitutes developmentally sophisticated, consciously reflective, analytic modes of thought (Tallis, 2004). For enactive proponents, behavior is constitutive of cognition, and the dynamics of an organism acting in real time, inextricably engaged with and coupled to its real-world context, should serve as conceptual grounding for our understanding of what cognition is (Di Paolo, 2009; Thompson, 2007). Cognition at

its most basic is something that organisms do in practice, through their embeddedness in the world; it is not an internal, behind-the-scenes computational processing of representations or subsequent driver of bodily movements (Hutto & Myin, 2018; Newen et al., 2018). For these proponents, cognition is practical, procedural knowing: “skillful know-how in situated and embodied action” (Engel et al. 2013, p. 202).

In contrast to orthodox computationalism, both extended and enactive conceptualizations of mind feature prominently in what Engel and colleagues (2013) have termed the “pragmatic turn” in cognitive science—a robust and revolutionary trend toward an “action-oriented paradigm,” bolstered by considerable empirical evidence (p. 202). This represents a true revolution in psychological science today that is being waged not through conservation of old ideas but through ongoing enactivist challenges to the fundamental tenets of computationalism. Even less radical strains of 4E cognition, such as extended conceptualizations of mind, reject the exaggerated, Pleistocene-program version of computationalism to which proponents of NEP continue to adhere (Clark, 2003).

Toward an Integrative Developmental Evolutionary Psychology Theory

Within evolutionary psychology, the privileged, standard-bearer status that has allowed NEP proponents to articulate the field’s conceptual underpinnings no longer seems tenable. As challenges to neo-Darwinist adaptationism in evolutionary biology and to computationalism in cognitive science continue to mount, well-established alternative approaches to evolutionary psychology, within psychology’s own broad ranks, warrant renewed consideration. In fact, a number of evolutionary psychologists have long decried NEP’s adaptationist and computationalist grounding, promoting instead a more complex, dynamic, enactivist grounding for the discipline (e.g., Barrett et al., 2014; Bolhuis et al., 2011; Burman, 2019; Lyon, 2006; Scher & Rauscher, 2003). These voices are in tune with current trends in both evolutionary biology and cognitive science. As such, they should be foregrounded in future conceptual discourse within evolutionary psychology. The field’s scientific currency demands it. In what follows, we offer some initial considerations on how to move forward with a developmental evolutionary psychology theory—DEPTH—that is responsibly grounded in modern evolutionary biology and cognitive science and that takes seriously what it means to be a malleable social mammal with a lengthy childhood—what it means, in other words, to be human.

The goal of integrating the evolutionary sciences into psychology should be to understand the unique evolutionary pathway that has brought humanity to its present moment (Henley et al., 2019; Small, 2008). A truly evolutionarily informed psychology needs to include an understanding of

the human species, its deep history as a social mammal situated in a broader, interrelated web of life, its multiple inheritances, its developmental processes, its basic needs, and the multiple systems involved in meeting those needs during development (Ingold, 2004; Narvaez, 2014). It would involve an understanding of people as dynamic, complex systems who self-organize in coordination with their experiences in the world (e.g., Thelen & Smith, 1994). It would integrate knowledge of epigenetics and plasticity in shaping human beings. It would synthesize understandings of an individual’s unique functional adaptation to their life circumstances and of the species’ evolutionary adaptations. It would have a sense of human potential and what optimal neurobiological functioning looks like in a wide variety of different contexts. NEP provides none of this. Central to this transdisciplinary endeavor is, at the very least, the examination of the role of niche provision in human development, the establishment of baselines for the range of species-typical human behaviors evident in the world today, and the integration of developmental plasticity and epigenetics. All play a role in the foundations for human functioning and could provide substantial dividends when systematically studied.

Examine Niche Provision

NEP’s focus on the inheritance of evolved psychological mechanisms distracts from accruing empirical evidence about how early relational experience (Organism \times Environment) constructs the person. Although niche *construction* has been acknowledged as part of our extragenetic inheritances (Odling-Smee, 1988), niche *provision* is an inheritance as well (Stotz & Narvaez, 2018). Every animal develops in a niche that contributes to the form of its physical, behavioral, and psychological characteristics (Gottlieb, 1998; West & King, 1987). Humanity’s evolved developmental niche (EDN) provides resources required for the construction of, for example, a healthy body (that resists infection), coordinated intelligence (critical for learning to find local food sources), and sociality (a critical feature of human adaptation), (Narvaez, 2014; Narvaez et al., 2013, 2014, 2016). Humans are social mammals, a line that emerged 20–40 million years ago with intensive early parenting practices (Konner, 2005). Human neonates are particularly immature, looking much like fetuses of other primates until 18 months of age (Trevathan, 2011); this observation led anthropologist Ashley Montagu to suggest that an external womb (extergestation) was needed during that time (Montagu, 1986). The human EDN for young children provides the resources needed for a healthy, well-functioning psychosocial neurobiology, including soothing perinatal experiences; extended on-request breastfeeding; maternal and allomaternal responsiveness to infant needs, including affectionate touch (keeping baby calm during

rapid growth); positive climate of support for mother and child; and self-directed play in the natural world with multi-aged playmates throughout childhood (Hewlett & Lamb, 2005; Hrdy, 2009). In the absence of EDN support, various systems may not develop properly, undermining the development of later-developing systems (Knudsen, 2004). For example, early life stress appears to impair the stress response for the long term (Lupien et al., 2009). Stress reactivity, a signal of dysregulation rooted in early life stress or trauma (van der Kolk, 2014; Shonkoff et al., 2012), makes social relations difficult and prosocial behavior even more so (Porges & Carter, 2010), in part because the stress response tends to focus energy on survival and self-protection (Sapolsky, 2004).

Establish Species-Typical Baselines

To embrace an evolutionary perspective, one must take a deep history view: “Phylogenetic history must be added [to explanations of the human psyche]; otherwise one fails to explain the peculiar potency that ontogenetic and cultural factors have in the shaping of the human mind as opposed to that of other animals” (Henley et al., 2019, p. 527). Important for human self-understanding is our emergence from social mammals whose offspring-rearing practices, such as breastfeeding and touch, led to increasing numbers of successfully reproducing progeny across generations, and so were retained for tens of millions of years (Konner, 2005). Civilization has been around no more than 20,000 years, or 1% of the existence of the genus *Homo*. Many people in industrialized societies, which represents a still smaller fraction of that 1%, raise children very differently than do people in traditional societies around the world, including a variety of small-band hunter-gatherer societies, which represent the type of society in which humans lived for over 1.9 million years (Lee & Daly, 2005). These traditional societies all share certain identifiable commonalities, in particular the early experiences they provide their offspring (Hewlett & Lamb, 2005). Data are accruing to demonstrate how important early experience, particularly components of the EDN, is for fostering well-functioning neurobiology, which grounds psychological functioning (Narvaez, 2014; van der Kolk, 2014; Witherington et al., 2018). For example, childhoods that are more EDN-consistent are associated with better physiological regulation (Tarsa et al., 2020) and mental health (Narvaez, Woodbury, et al., 2019; Narvaez et al., 2016).

It is important to be clear on baselines for drawing conclusions about human development. It may be time to rethink using individuals with an EDN-inconsistent childhood as prototypical specimens for gathering information on the human species generally. Lacking a perspective of deep history, many scholars, including NEP theorists, take as normal human nature the characteristics of individuals

from industrialized and westernized societies, including dysregulation, selfishness, and aggression (e.g., Dawkins, 1976; Thornhill & Gangestad, 1996), even though their early experiences can be viewed as EDN-inconsistent (Narvaez et al., 2013). Anthropologists have noted a different set of characteristics among individuals raised within EDN-consistent contexts such as intuitive cooperation and generosity, high autonomy with high communalism, and with no coercion and little competition (e.g., Ingold, 2005; Sorenson, 1998). Many characteristics that NEP proponents study (because they are assumed to represent human nature) such as concern for fatherhood and mate selection (e.g., see Buss, 1994), are not apparent among nomadic foragers, who tend to be promiscuous and matrifocal rather than patriarchal (Hrdy, 2009; Marlowe, 2004). Moreover, small-band hunter-gatherer groups often consist of kin and non-kin, with membership changing by the day, with interdependence across groups as the norm (Hill et al., 2011).

The EDN has been around for 20–40 million years as part of the social mammalian line, with slight revisions by hominids (e.g., multiple responsive caregivers, variation on breastfeeding length). Consequently, the EDN could be used to develop an exceptionally good heuristic for determining a baseline for species-typical development, rather than selecting a baseline out of thin air or assuming that research participant behavior is adaptive (Narvaez & Witherington, 2018). Generalizing from contemporary human behavior in industrialized societies where EDN-inconsistent childhoods are widespread—as psychological research, including work in NEP, often does (Henrich et al., 2010)—may misinform psychologists about human potential.

Integrate Developmental Plasticity and Epigenetics

In addition to using misleading baselines, NEP misleads on the causes of contemporary human behavior by looking for these causes in genetic inheritance while ignoring developmental factors (Ingold, 2006; Lewontin et al., 1984; Moore, 2002; Noble, 2006; Oyama, 1985). Evolutionary theory should be used to advance our understanding of human beings as malleable social mammals who undergo a lengthy period of development (2 to 3 decades). The naïve view of phenotype causation advanced by NEP is simply inadequate for the task. For example, genetic action is a much more complex story than acknowledged by NEP proponents. Gene regulation involves not only the activation of a gene, but the creation of mRNA via splicing processes and the insertion, deletion, or exchange of single nucleotides of the RNA, all of which can be characterized as a type of molecular epigenesis involving more than the genome alone (Stotz & Griffiths, 2018). Molecular epigenesis involves “recruitment, activation and transportation of transcription, splicing, and editing factors [which] renders them functional and allows the environment to have specific effects

on gene expression” (Stotz & Griffiths, 2018, p. 110). Thus, gene regulation involves not only genetics, but also, via epigenetics, factors much further afield, including hormones, diets, parenting, and influences from the broader social environment. Beyond genes and gene-related effects, humans inherit cell and body plans (Margulis, 1998), culture and ecology (Jablonka & Lamb, 2005), as well as developmental systems for raising the young (Gottlieb, 1998), all of which are deeply integrated and together escalate the influence of experience on development while increasing the importance of developmental plasticity to evolutionary change. Psychological research and theory have begun to attend to the impact of developmental system differences in light of basic needs fulfillment (e.g., for warm responsive care in infancy) on shaping psychosocial neurobiological functioning (e.g., attachment; Schore, 2019). Initial data suggest that humans might be much more epigenetically shaped and more plastic than other animals, especially early in life (Gómez-Robles et al., 2015). The complexity of inheritances and the dynamic nature of development and human plasticity are not addressed by NEP, but need to be by a more biologically credible theory of evolutionary psychology.

These three realms of study overlap and require systematic investigation but hold promise for reshaping evolutionary psychology in helpful ways. First, organisms self-organize around experience, so it matters what that experience entails. For example, human infants organize their psychosocial neurobiology around the care received, for better or for worse. Adverse childhood experiences (ACES) are on the rise in the United States, leading to illness and early death (Felitti & Anda, 2005). Denial of the evolved developmental niche in early life may provoke toxic stress, which is known to impair multiple neurobiological systems with potentially long-term effects on physiological and psychological health (e.g., Lanius et al., 2010). NEP does not contribute to our understanding of these processes, but DEPTH very well could. Second, as noted by others, psychology (along with some other disciplines) has often used samples from WEIRD (Western, European, Industrialized, Rich, and Democratic) countries when seeking baselines for species typicality. This practice undergirds discrimination toward non-WEIRD populations, despite the fact that non-WEIRD populations maintain more cultural and biological diversity, a hallmark of evolutionary processes (Díaz et al., 2019). NEP seems to draw their baselines from similarly skewed samples. Third, if we understand the nuances of the neurobiological plasticity of the human animal, unlike NEP we can avoid the fatalism of a limited developmental focus and better attend to how individuals self-organize through epigenetic processes. When we understand ontogenetic mechanisms, we can establish what the relations between optimal neurobiological development and psychological functioning look like, and what is necessary for flexible resilience. We can focus on prevention as well as intervention to enhance human potential.

In response to a deeper evolutionary perspective on the self-organizing of human beings, psychologists may also need to address the sociopolitical systems that undermine or condone ill being, especially among the less privileged. By taking advantage of the broader developmental-evolutionary approach we advocate, psychologists can employ a deep-history evolutionary perspective to help determine how to promote the well-being of humans and nonhumans and to foster a sustainable future (Kidner, 2001).

Conclusion

The goal of integrating evolutionary sciences into psychology should be to understand the unique evolutionary and developmental paths of human beings. A developmental evolutionary psychology theory (DEPTH) can do just that. How do human beings come to be shaped by processes that are influenced by our evolutionary history, but also by more proximal contingencies in our developmental histories, and the current state of our bodies and contexts? Although ideas and phenomena considered by narrow evolutionary psychology (NEP) theorists are worth considering, we have indicated NEP’s restricted focus and deficient conceptual foundations. So much is left out. It is quite problematic that many psychologists and nonpsychologists have come to think of NEP as the only way in which to bring evolutionary ideas to bear on psychological questions. Although NEP bills itself as a revolutionary theory applicable to all of psychological science, it is in fact built on an outdated framework and, as such, should not be considered the agreed-upon perspective of all theorists interested in seeing evolutionary thought represented in psychology. Instead, it is time to recognize the heterogeneity of ideas available about how evolution should be brought to bear on psychological questions (Scher & Rauscher, 2003). Evolutionary processes are vital for explaining human behavior and integrating across biology, culture, and development. But an evolutionary psychology too out of step with current developments in evolutionary biology, cognitive science, genomics, and other disciplines cannot adequately advance such important interdisciplinary integrations. NEP’s reliance on neo-Darwinian adaptationism, staunch computationalism, and neglect of appropriate baselines for human normality and development all render NEP inadequate for handling the all-important application of evolutionary theory to the study of human psychological functioning and well-being.

Narrow evolutionary psychology’s focus on survival and reproduction leaves out *thriving*, which is required for natural selection—a family line must thrive to out-compete rivals over generations. What is important for thriving offspring? The Evolved Developmental Niche may establish a “cultural commons” for shaping human nature toward cooperation and openness, crucial features

of our adaptive past (Hrdy, 2009). Societies that provide the EDN are characterized by self-regulation, cooperation, social and emotional intelligence, and humble self-confidence (Fry, 2013; Ingold, 2005; Lee, 2018; Sorenson, 1998). One proposal is to reset the baseline for normal human nature away from the “nasty and brutish” perceptions advanced by writers in the last millennium (Hobbes, 1651; Spencer, 1850). Once we shift our focus to prosocial human characteristics and to developmental processes—to DEPTH—we will be motivated to study how such traits are shaped initially by early life experience (when human beings are particularly developmentally plastic via epigenetic processes), and subsequently maintained by ongoing needed support throughout life.

The questions that a developmental evolutionary psychology would ask are almost the flip side of what is typically studied by narrow evolutionary psychologists. Rather than puzzling about altruism, the question would be what sorts of evolutionary and developmental processes explain why there is little or no concern about “altruism” in deeply cooperative societies that do not perceive “other” to any large degree, but experience unity with a sentient world full of persons, even rivers, mountains, and winds as a part of the commonsense or Ecological Self (Harvey, 2017; Narvaez, Four Arrows, et al., 2019). What evolutionary and developmental processes led some humans (the dominant ones today) to become so uncooperative with the natural world, so much so that they/we have broken previously resilient ecologies all over the planet? Why did they begin to think of themselves as separate from and superior to the natural world, unlike most prior humans and societies of the world? For a species whose sociality across species and with kin and nonkin has been adaptive, how do people become accustomed to disconnection, distrust, and antisociality? These are questions that could be considered and addressed by a more integrated, broad-based evolutionary psychology. Narrow evolutionary psychology is not up to the task, but a developmental evolutionary psychology theory is.

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